

TAXONOMY AND VARIATION OF THE *LOPIDEA NIGRIDIA* COMPLEX OF WESTERN NORTH AMERICA (HETEROPTERA: MIRIDAE: ORTHOTYLINAE)

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ABSTRACT.—External morphological variation in the *Lopidea nigridia* "complex" of western North America was examined using principal component analysis and showed continuous variation among populations in most characters. External morphology did not parallel paramere structure and did not substantiate previously recognized species. There was little correlation between dorsal coloration and paramere structure. Cluster analysis (UPGMA) using paramere and color characters failed to group populations coded as the same species and also failed to group all specimens of any one population. The variation in structure of the parameres and vesicae among populations of the *nigridia* complex was no greater than the interpopulational variation of these structures in the congeneric species *marginata* Uhler.

Lopidea nigridia Uhler is treated as a polytypic species comprising three subspecies: *Lopidea nigridia nigridia* Uhler, a fuscous-white form from the sagebrush steppe of the Great Basin and the chaparral of southern California; *Lopidea nigridia serica* Knight, a solid red form from the eastern slopes of the Rocky Mountains from Alberta to Colorado and east across the northern Great Plains to southern Manitoba; *Lopidea nigridia aculeata* Van Duzee, a polymorphic form varying from solid red to fuscous red and white from the Cascade Mountains and eastern slopes of the coastal ranges of British Columbia, Washington, and Oregon, the Blue and Wallawa mountains of Oregon and Washington, and throughout the Coastal and Sierra Nevada ranges of California.

The following new synonymies are created: *Lopidea nigridia nigridia* Uhler = *Lopidea raineri* Knight, *Lopidea scullei* Knight, *Lopidea rolfsi* Knight, and *Lopidea wilcoxi* Knight; *Lopidea nigridia aculeata* Van Duzee = *Lopidea nigridia hirta* Van Duzee, *Lopidea usingeri* Van Duzee, *Lopidea discreta* Van Duzee, *Lopidea fallax* Knight, *Lopidea yakima* Knight, *Lopidea audeni* Knight, *Lopidea eriogoni* Knight, *Lopidea calcaria* Knight, *Lopidea chamberlini* Knight, *Lopidea angustata* Knight, *Lopidea rubrofusca* Knight, and *Lopidea flavicostata* Knight and Schaffner; *Lopidea nigridia serica* Knight = *Lopidea uedleri* Akingbolungbe.

Lopidea Uhler comprises over 100 described species from Central and North America (Henry and Wheeler 1988). Most are large (>5.0 mm), brightly colored plant bugs displaying some pattern of contrasting red-black or yellow-black coloration. There is no taxonomic revision of the genus, but most species were described in a series of papers by Knight (1917, 1918a, 1918b, 1923, 1962, 1965) and Knight and Schaffner (1968, 1972).

Many species are superficially very similar in habitus, and most have been distinguished by the form of the right paramere. This structure is relatively uniform in any given species but extremely variable in size and form among different species of *Lopidea*. It appears that this is the most valuable diagnostic character available for distinguishing different species of *Lopidea*, aside from the vesica.

External and internal male genitalia are now widely used to differentiate taxa in certain groups of Heteroptera, but detailed studies of the variation in these structures are

lacking. In the Orthotylini, males often have elaborate parameres and vesicae, and differences in these structures are used to define species (Kelton 1959, Stonedahl and Schwartz 1986). The limits of the variation of these structures in populations and throughout the range of species need to be defined.

Several species of *Lopidea* described from western North America have parameres very similar if not identical to an earlier described species, *Lopidea nigridia* Uhler. I undertook the present study to resolve the taxonomy of this group, which I refer to as the *nigridia* "complex." In this paper I describe the morphological, genitalia, and color variation within this complex and document the characters that unite it as a single taxonomic unit.

MATERIAL AND METHODS

Over 3,000 specimens from throughout the range of *Lopidea* were examined during the course of this study. Male specimens with

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"*nigridia* type" paramere morphology and the associated females were sorted by grouping series that displayed common patterns of color, size, and paramere morphology. Locality data from all specimens examined are available in the author's doctoral dissertation, Oregon State University.

Male genitalia of specimens from different geographic localities within each group were examined. Techniques for the dissections generally followed Kelton (1959). To determine the infraspecific variation in the structures, I compared variation within and among the populations with the closely related species *marginata* Uhler. I had previously determined that the female genitalia are too uniform throughout the genus to provide information at the specific and subspecific levels.

Morphological variation in this complex was examined by recording metric data from 139 males from the following localities (*N* follows each locality): MEXICO: Baja California Norte, Parque San Pedro (7); CALIFORNIA: Los Angeles Co., El Segundo (10); Mono Co., Leavitt Meadow (10); Trinity Co., Buckhorn Mt. (14); Tuolumne Co., Yosemite Park (10); COLORADO: Elbert Co., Kiowa (11); NEVADA: Elko Co., (7); OREGON: Polk Co., Dallas (2); Crook Co., Ochoco Summit (10); Deschutes Co., Metolius River (5); Harney Co., Pike Creek (5); Jackson Co., Pinehurst (10); WASHINGTON: Pierce Co., Mt. Adams (10); Pierce Co., Mt. Rainier (10); WYOMING: Carbon Co. (14).

Specimens from Mt. Adams and Mt. Rainier are topotypes of *L. rolfsi* Knight and *rainieri* Knight, respectively. Samples from the rest of the populations were selected to cover the range of type localities as well as color and paramere variation of the nominal species in the *nigridia* complex.

An ocular micrometer was used to measure eight external characters: rostral length (RL) (because the rostrum was often bent at the joints, making its total length difficult to ascertain, only the length of the last three segments was measured); hind tibial length (HTL); length of antennal segment 1 (A1); length of antennal segment 2 (A2); width of head across eyes (HW); maximum length of the pronotum (PL); anterior width of the pronotum (APW); posterior width of the pronotum (PPW). To examine the multidimensional morphological

TABLE 1. Correlations between the first two principal components and the morphometric measurements of male *Lopidea nigridia*.

Character	PC I	PC II
Rostral length	0.636	-0.731
Hind tibial length	0.896	0.129
Antennal segment 1	0.912	0.173
Antennal segment 2	0.870	0.258
Head width	0.892	-0.135
Pronotal length	0.941	0.032
Anterior pronotal width	0.847	0.002
Posterior pronotal width	0.892	-0.031

variation in these populations, I applied principal component analysis to the measurements (PCA; Morrison 1976) using SYSTAT (Wilkinson 1986). Although a logarithmic transformation usually results in a more nearly normal distribution of the data (Sokal and Rohlf 1981), it can also distort the multivariate space described by the measurements (Ricklefs and Travis 1980). Analyses using both raw and log-transformed data produced almost identical results; therefore, only results using raw data are presented here.

Because most of the described species in the *nigridia* complex were based on differences in color and male paramere morphology, I recorded eight characters of color and paramere morphology from the 139 specimens used in the morphometric analysis. Color characters were calli, scutellum, embolium, and cuneus, and they were coded for black, red, or white. Paramere characters included angle of the dorsal spine (CA), straight, slightly angled, acute; number of serrations on apex of paramere (SER); number of spines/bifurcations at apex of dorsal spine (SPIN); development of secondary spine on body of paramere (SECSPIN). These data were standardized and analyzed by SPSS/PC Hierarchical Cluster Analysis using UPGMA on distance matrices of squared euclidean distances.

RESULTS

Principal Component Analysis

The first two principal components accounted for 84% of the morphological variation among individuals. The first component (PC I, 76.1%) reflects the general size variation among individuals; all variables were positively correlated with PC I (Table 1). PC II

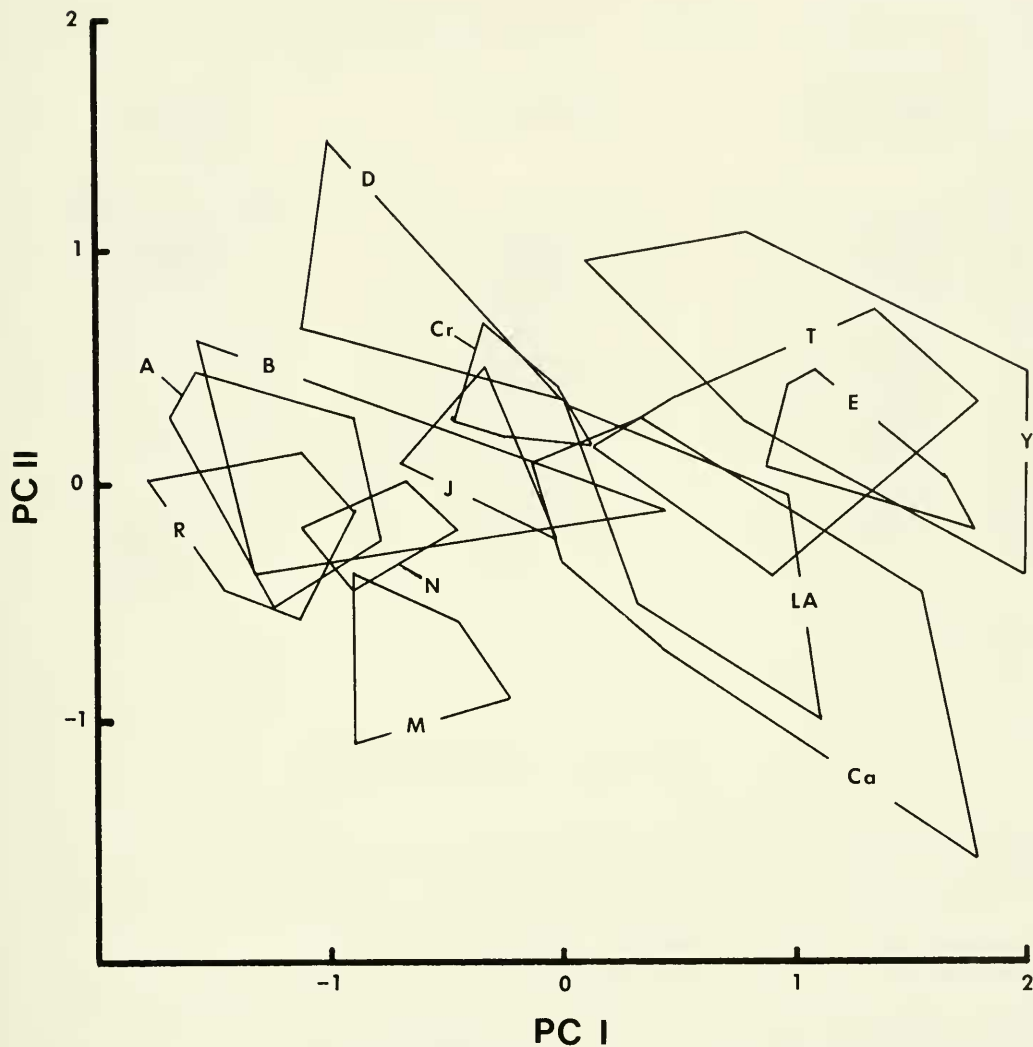


Fig. 1. Morphological variation of *Lopidea nigridia* Uhler based on principal component analysis. Populations are plotted on the first (PC I) and second (PC II) principal components, enclosed in polygons connecting the outlying individuals of each sample. Abbreviations: R = Mt. Rainier, WA (*L. n. nigridia*); A = Mt. Adams, WA (*L. n. nigridia*); Ca = Carbon Co., WY (*L. n. serica*); N = Elko Co., NV (*L. n. nigridia*); B = Baja California Norte (*L. n. aculeata*); J = Jackson Co., OR (*L. n. aculeata*); Cr = Crook Co., OR (*L. n. aculeata*); LA = Los Angeles Co., CA (*L. n. nigridia*); M = Mono Co., CA (*L. n. nigridia*); E = Elbert Co., CO (*L. n. serica*); T = Trinity Co., CA (*L. n. aculeata*); Y = Yosemite Park, CA (*L. n. aculeata*); D = Deschutes Co., OR (*L. n. aculeata*).

(7.9%) reflects an inverse relationship between RL and A2. To illustrate the distribution of populations in the morphological space described by the principal components, individuals were plotted on axes described by PC I and PC II and populations were enclosed in polygons by connecting the outlying individuals with lines (Fig. 1).

This analysis illustrates some of the morphological differences among populations.

For example, the Yosemite population (Y) is composed of large individuals with relatively long antennae and short rostra. The Mono County population (M) is composed of relatively small individuals with short antennae and long rostra. These two populations examined separately are quite distinct; they do not overlap in overall size and have differently proportioned antennae and rostra. However, both populations overlap other groups to

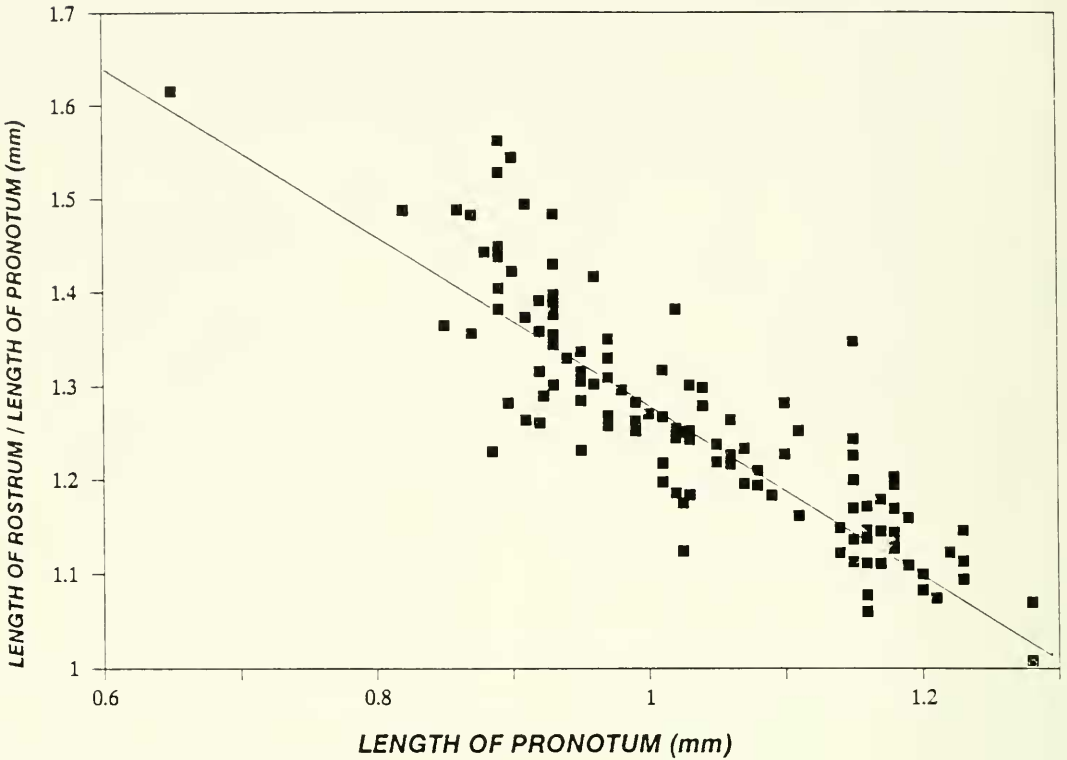


Fig. 2. Relationship between relative length of the rostrum (rostrum length/pronotum length) and pronotum length in *Lopidea nigridia*; $y = 2.1777 - 0.884x$, $r^2 = 0.757$, $N = 128$.

some degree, creating a continuum of morphological variation in all dimensions. This pattern makes it difficult to clearly segregate a population or groups of populations based on external morphology alone.

There was no clear pattern of morphological variation with regard to geography. The largest individuals were found in two California populations (Y, T), the Wyoming population (Ca), and the Colorado population (E). Individuals with short antennae and long rostra were found in the Wyoming population (Ca) and a California population (M). The two most morphologically similar populations were Wyoming (Ca) and Los Angeles County (LA).

Not all coefficients of variables in the PCA analysis were of equal magnitude, suggesting allometric relationships among the variables. For example, PC I represents general size variation among individuals, and rostral length has the lowest correlation with PC I (Table 1). This suggests that as size increases

rostral length increases more slowly than other characters.

The significance of this pattern can be seen by examining the relationship of rostral length to the best single measure of size, pronotal length. The relative length of the rostrum (RL/PL) decreases with increasing size (Fig. 2). Very small individuals have rostra that are 1.5 times the length of the pronotum, whereas very large individuals have rostra that are only equal to the length of the pronotum. This has important implications regarding the taxonomic value of these and similar characters, such as the distance the rostrum extends posteriorly on the sternum. In very small individuals of the *nigridia* complex the rostrum extends to or slightly beyond the metacoxae, whereas in large individuals the rostrum may not reach the mesocoxae.

Color Pattern

Dorsal coloration of individuals from any one series was usually uniform, but color

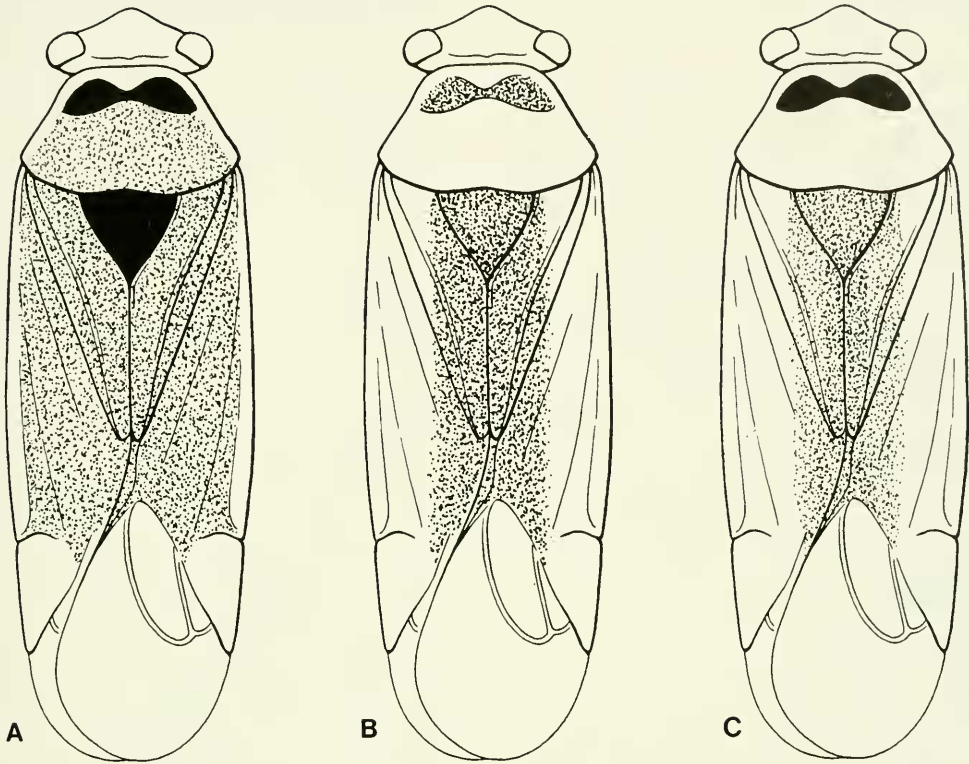


Fig. 3. Variation in dorsal color pattern of *Lopidea nigridia* Uhler: A, fuscous-white color pattern characteristic of *L. n. nigridia* Uhler; B, fuscous-red-white color pattern characteristic of *L. n. aculeata* Van Duzee; C, solid red color pattern characteristic of *L. n. serica* Knight. Stippled areas represent fuscous coloration; gray areas represent red coloration.

varied dramatically among collections. At one extreme is a red form that is uniformly brick red with slight to moderate infuscation on the clavus. At the other extreme is a fuscous-white form with the clavus and corium predominantly to completely reddish fuscous and the embolium and cuneus pale white (Fig. 3). Color variants intermediate of the two extremes also occur.

The color patterns of the *nigridia* complex also occur in several related sympatric species. *Lopidea marginata* Uhler displays very similar color variation, with some populations composed of solid red individuals, while in other populations the clavus and corium are infuscated and the embolium and cuneus pale white.

The different color forms in the *nigridia* complex do not appear to be segregated with regard to host plant west of the Rocky Moun-

tains, and both color extremes have been collected from near sea level in southern California to >5,000 ft. elevation in the Sierra Nevada and Cascade Mountain ranges. The most conspicuous geographic patterns are the absence of the red form from the Intermountain Sagebrush Province and the absence of the fuscous-white form from the Great Plains short-grass prairie (Fig. 4). This latter pattern also seems to correspond to a switch in preferred host plants from *Lupinus* to *Astragalus* (see Biology).

Paramere Structure

There were few correlations between color and paramere variables and morphology. PC I, representing size, was negatively correlated with the number of serrations on the paramere and all color variables (Table 2). In general, populations of large individuals also

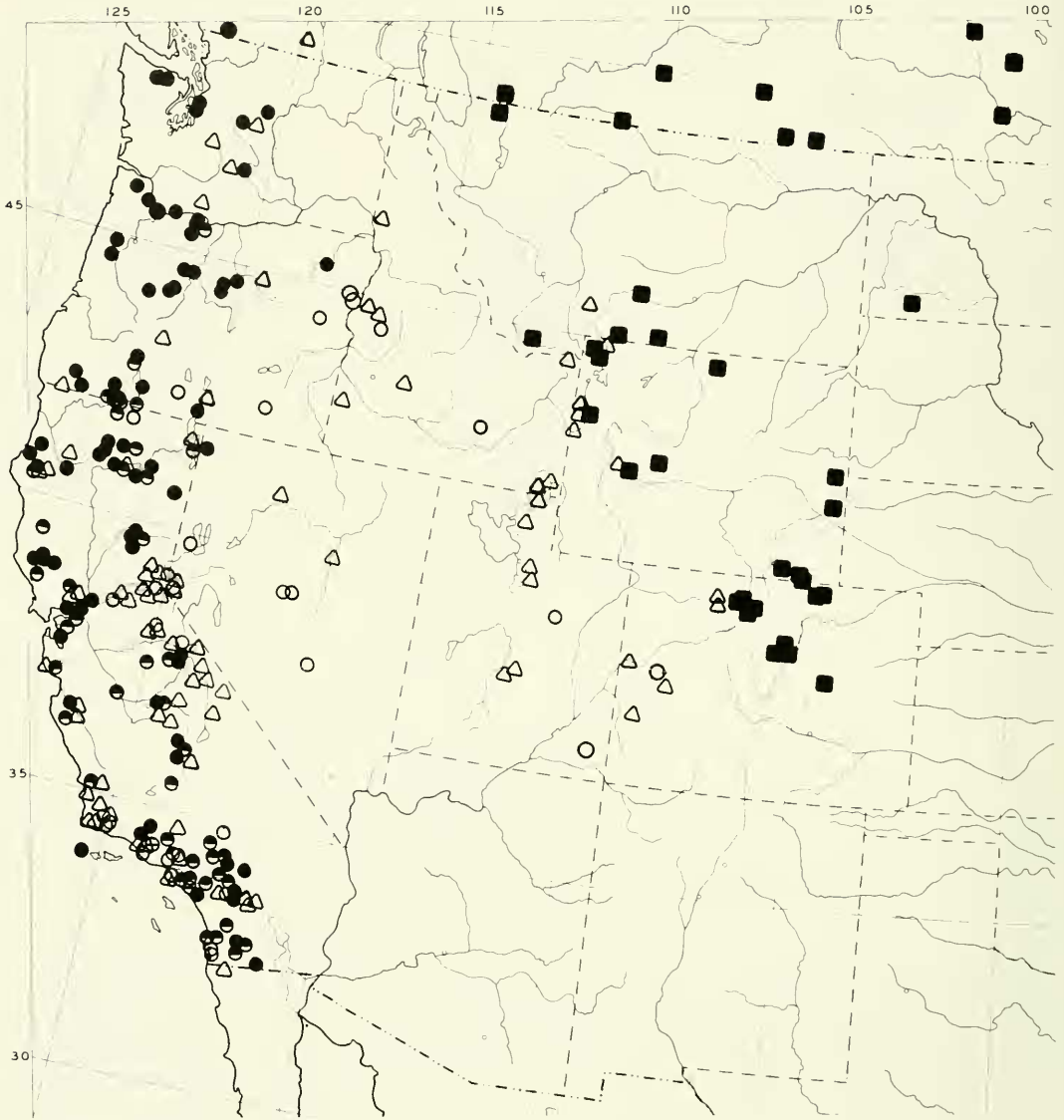


Fig. 4. Distribution of subspecies and color forms of *L. nigridia* Uhler in western North America: triangles = fuscous white form of *L. n. nigridia* Uhler; open circles = more reddish color form of *L. n. nigridia* Uhler; solid circles = solid red color form of *L. n. aculeata* Van Duzee; half solid circles = red-white color form of *L. n. aculeata* Van Duzee; solid squares = *L. n. serica* Knight.

tend to have more serrations and to be solid red with no white on the embolium or cuneus, and smaller individuals have fewer serrations and are more fuscous with a white embolium and cuneus. Although this trend was apparent for most specimens I examined, it was not always true; individuals from Deschutes Co., Oregon (D), are relatively small and yet are solid red in color, and I have seen very large

specimens from Santa Barbara Co., California, that have a light embolium and cuneus.

Many characters of the right paramere formerly used to distinguish species within the *nigridia* complex vary among individuals within a population. For example, *wilcoxi* Knight was distinguished from *rainieri* Knight by the absence of a secondary spine in *wilcoxi*. In only two populations examined

TABLE 2. Pearson correlation coefficients between the first two principal components and paramere and color characters of male *Lopidea nigridia*. * = significant at alpha < .05; ** = significant at alpha < .001; NS = not significant (alpha > .05).

Character	PC I	PC II
CA	-0.157 NS	-0.121 NS
SER	-0.361 **	-0.066 NS
SPIN	-0.020 NS	-0.054 NS
SECSPIN	-0.067 NS	-0.110 NS
CALLI	-0.308 **	0.195 *
SCUT	-0.207 *	0.180 *
EMBOL	-0.594 **	0.072 NS
CUN	-0.564 **	0.116 NS

did all individuals either have or completely lack this structure. Some populations in the Siskiyou Mountains of California and Oregon contain individuals with a distinct toothed hook ventrally on the apex, used by Knight (1965) to distinguish *calcaria* Knight and *erigoni* Knight. Other individuals from the same series lack this structure and display parameres more similar to other described species in the complex. Figure 5 illustrates the extent of variation of the right paramere seen in the *nigridia* complex. The only aspect of the right paramere common to all populations and absent in other species of *Lopidea* is the presence of the elongate dorsal spine at the apex.

Examination of the left paramere and internal genitalia corroborated the patterns seen in the right paramere. The left paramere is structurally less complex than its counterpart and thus shows less variation. The medial flange is digitiform, with its distal end usually slightly clavate and free from the main body of the paramere. The vesica bears a slender, slightly curved ventral spicula, toothed at the apex and with a slight swelling at its midpoint. The dorsal spicula is short, broadly lanceolate, toothed, and slightly curved. The variation in these structures between color forms of the *nigridia* complex is no greater than the infraspecific variation seen in other species. This is illustrated in Figure 6, where genitalic structures of a fuscous-white and a red form of *nigridia*, both from Wyoming, are compared with the same structures from individuals of *marginata* Uhler from Oregon and Baja California. The dorsal spicula is usually shorter and straighter in the fuscous-white color form. The dorsal spicula, however, varies in shape

from straight and blunt to curved and evenly pointed (Fig. 7); it also shows considerable variation in other species of *Lopidea*.

Cluster Analysis

This analysis demonstrates the difficulty of separating groups within the *nigridia* complex based on color and paramere characters. In no case were all individuals from one population found to be most similar to each other; at least one individual was always grouped with those from another population. In most cases, individuals from any given population were scattered throughout the dendrogram. For example, the Mt. Adams population (A) had individuals placed in four of the five major clusters (Fig. 8A).

The cluster analysis did not identify groups composed of individuals that I determined as being the same color form. For example, all individuals from Crook Co. (Cr), Trinity (T) (Fig. 8B), and Jackson Co. (J) (Fig. 8A) represent the solid red form; however, Cr specimens were grouped in the uppermost cluster, T specimens in the next lower cluster, and J specimens in the middle three clusters. Similarly, specimens representing the fuscous-white form were also found in all of the major clusters. This analysis further suggests that grouping specimens within the *nigridia* complex based on color and paramere morphology gives equivocal results.

TAXONOMY

All specimens examined in this study clearly belong to a monophyletic group. They are united by the presence of an elongate dorsal spine on the apex of the right paramere; a free, digit-shaped medial flange on the left paramere; and a slender, slightly spindle-shaped ventral spicula. These are derived characters found in no other species of *Lopidea*. In addition, all specimens are believed to be conspecific for the following reasons. Populations or groups of populations cannot be distinguished by combinations of external morphological measurements. Although populations display considerable color variation, color is not highly correlated with external or paramere morphology, and similar color variation is seen in related species. Most characters of the right paramere vary among individuals from any population. Only characters

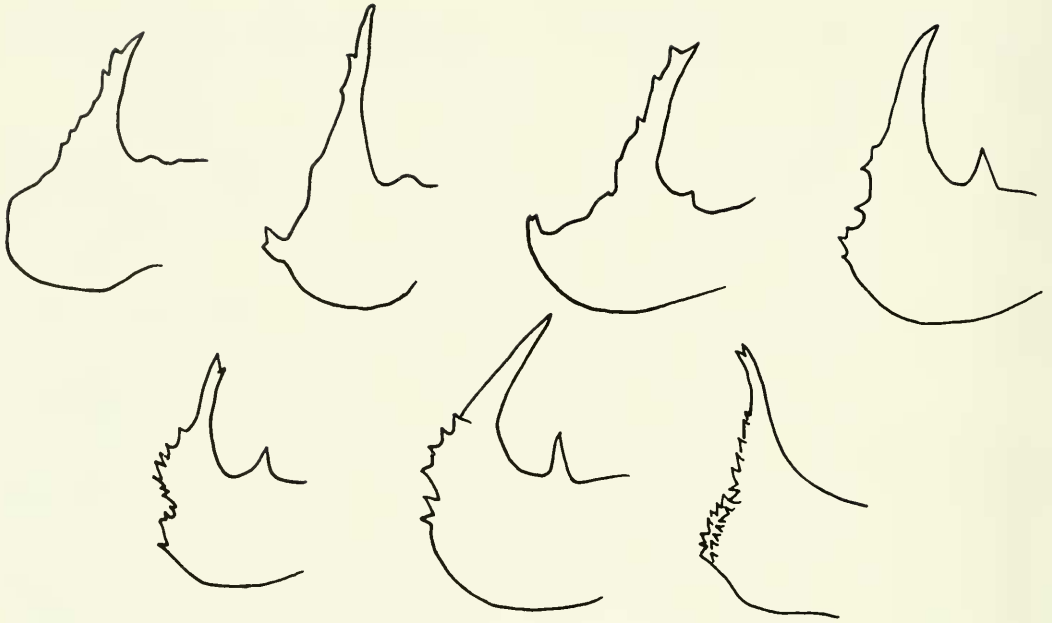


Fig. 5. Variation of right paramere in *Lopidea nigridia* Uhler. Drawn in posterolateral view.

common to all populations, such as the elongated spine on the dorsal apex of the right paramere and the digit-shaped medial flange on the left paramere, also corresponded with unique characters of the male vesica.

I have also examined the type specimens of all nominal species in the *nigridia* complex and have determined, using the above criteria, that they also are conspecific with *nigridia* Uhler. I interpret *nigridia* as being a polytypic species comprising three subspecies segregated to some degree by geography and/or habitat. I have elected to use the subspecies category for these taxa because, based on the available data, it adequately describes the broad geographic patterns of the color forms. I have retained the subspecies *L. n. nigridia* Uhler for the Intermountain, fuscous-white form and *L. n. serica* Knight for the solid red, eastern Rocky Mountain and prairie form. I also recognize *L. n. aculeata* Van Duzee as a polymorphic form of the Pacific Coast states. Below I provide a complete synonymy for *nigridia* and its subspecies. All lectotype and holotype label data are given verbatim.

Lopidea nigridia Uhler

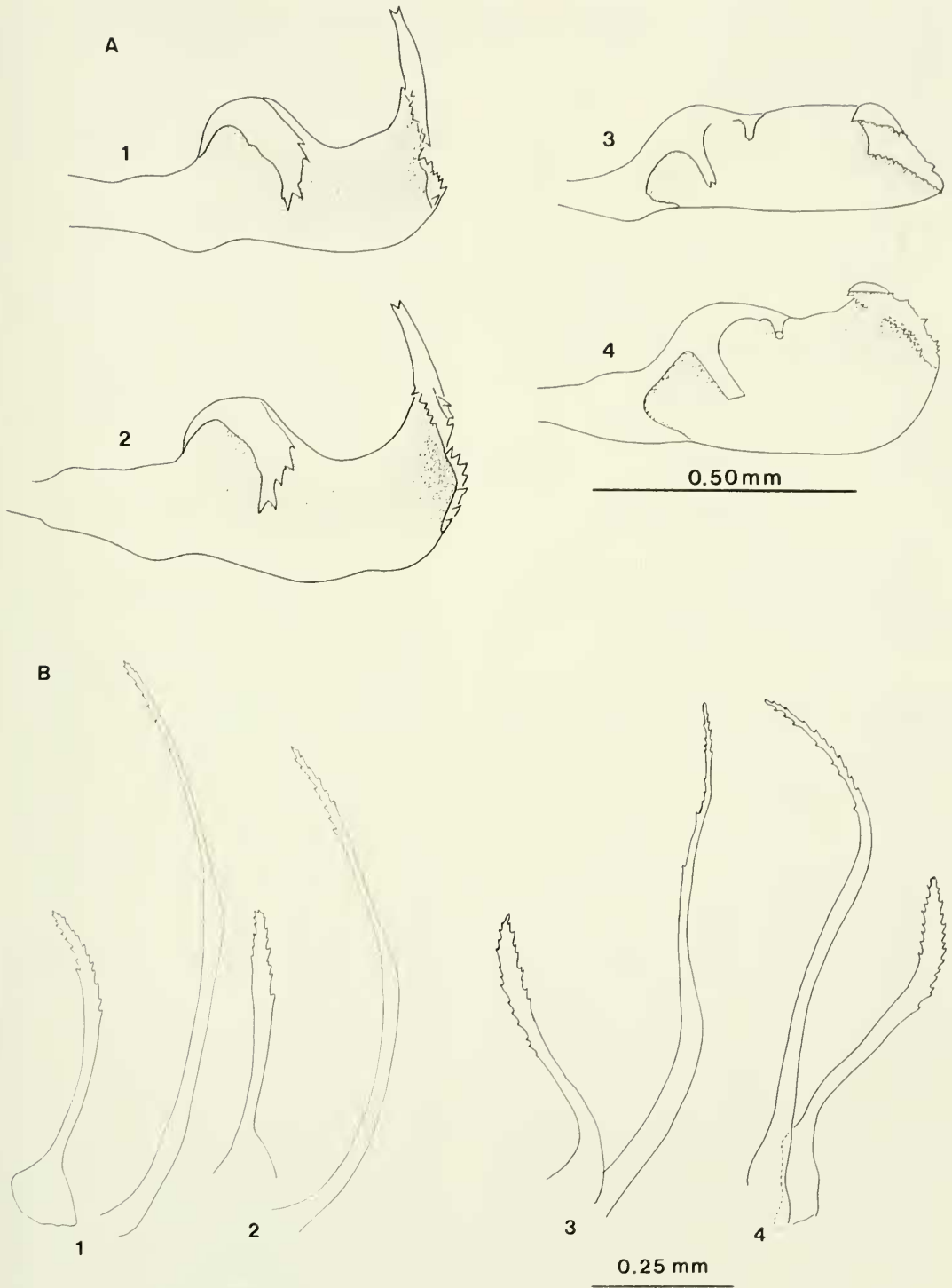
Lopidea nigridia Uhler, 1895:30 (n. sp., desc.).

Lopidea nigridea: Osborn, 1895:233 (dist.). Van Duzee, 1914:25 (list). Van Duzee, 1916:241 (cat.). Van

Duzee, 1917:384–385 (cat.). Van Duzee, 1921:127 (n. subsp.). Knight, 1923:69 (fig.). Van Duzee, 1933:96 (note). Carvalho, 1958:87 (cat.). Knight, 1965: 8–10 (fig.). Akingbohunge, 1972:842 (note). Henry and Wheeler, 1988:422 (cat.).

LECTOTYPE (designated here).—♂, Colo. 1387 [1387 = Steamboat Springs, Col. July C. F. Baker, ex. *Delphinium occidentale*]; *Lopidea nigridea*, det Knight; LECTOTYPE *Lopidea nigridia* Uhler, det A. Asquith; deposited in the USNM.

HOLOTYPE OF SYNONYMS.—*Lopidea aculeata* Van Duzee: ♂, Seattle, Wash.; W. M. Giffard, 7-VII-17; (CAS). *Lopidea angustata* Knight: ♂, Antioch Calif., Sand Dunes, June 4, 1942, H. A. Scullen; (USNM). *Lopidea audeni* Knight: ♂, Midday Valley, Merritt B.C., July 1925, K. F. Auden; (USNM). *Lopidea calcaria* Knight: ♂, Crater Lake, Ore., South Rim, 7100 ft elev., July 29, 1930; H. A. Scullen; (USNM). *Lopidea chamberlini* Knight: ♂, Whitman N. F., OR, VII-22-14; W. J. Chamberlin Collector; (USNM). *Lopidea discreta* Van Duzee: ♂, Huntington Lake Ca., July 26, 19; Fresno Co. 7,000 ft.; E. P. Van Duzee Collector; (CAS). *Lopidea eriogoni* Knight: ♂, Drake Peak, Lake Co., Ore., 7,850 ft. elev., July 26, 1930; (USNM). *Lopidea fallax* Knight: ♂, below Mt. Springs, San Diego Co. Calif., June 11, 1915, Harold



Figs. 6A-B. Comparison of genitalie structures of *Lopidea* species: A, right paramere: 1, *L. n. nigridia* Uhler, Yellowstone Nat. Pk., WY; 2, *L. n. serica* Knight; 3, *L. marginata* Uhler, Benton Co., OR; 4, *L. marginata* Uhler, Baja California Norte. B, Spiculae: species as in A.

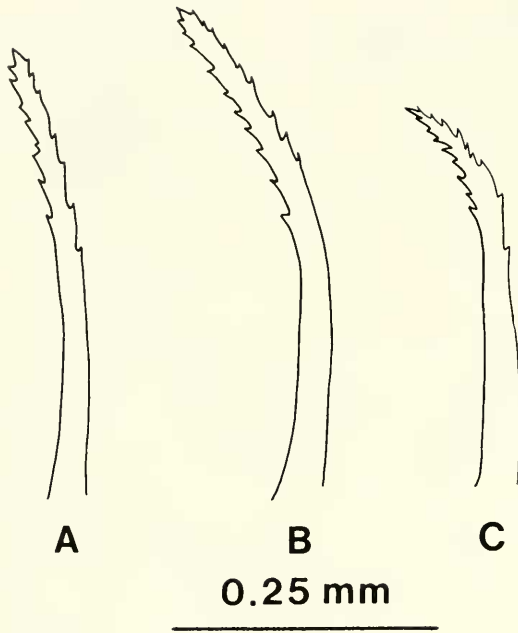


Fig. 7. Variation of the dorsal spicula in *Lopidea nigridia* Uhler: A, *L. n. nigridia* Uhler, Lander Co., NV; B, *L. n. serica* Knight, Carbon Co., WY; C, *L. n. aculeata* Van Duzee, Trinity Co., CA.

Morrison; (USNM). *Lopidea flavicostata* Knight and Schaffner: ♂, Camino, Calif., July 10, 1965, H. H. Knight; (USNM). *Lopidea medleri* Akingbohunge: ♂ (holotype not examined) Eau Claire Co., Fairchild, Wisc., 7-15-63, J. T. Medler (UWM). *Lopidea nigridea hirta* Van Duzee: ♂, San Miguel Isl., Cal., V-20-1919; EP Van Duzee Collector; (CAS). *Lopidea rainieri* Knight: ♂, Mt. Rainier, Wash., Aug. 14, 1931, H. H. Knight; (USNM). *Lopidea rolfsi* Knight: ♂, Mt. Adams Wa., Aug. 3 1930, A. R. Rolfs; (USNM). *Lopidea rubrofusca* Knight: ♂, Monticello, Ut., 6-18-33; G. F. Knowlton Collector [the name written on the holotype label is spelled "rubrofuscata" but was published as *rubrofusca*] (USNM). *Lopidea sculleni* Knight: ♂, Cornucopia, OR, 7,100', July 25, 1936, H. A. Scullen, col.; (USNM). *Lopidea serica* Knight: ♂, Ft. Collins, Col. 6-28-00; (USNM). *Lopidea usingeri* Van Duzee: ♂, Oakland Rec. Camp, Cal., VII-20-27; Toulumne Co.; R. L. Usinger Collector; (CAS). *Lopidea wilcoxi* Knight: ♂, Mt. Rainier, Wa., VII-13-'31, sunrise, 6,318'; J. Wilcox, Coll.; (USNM). *Lopidea yakima* Knight: ♂, Olympia, Wash., Aug. '93; (USNM).

DIAGNOSIS.—*Lopidea nigridia* belongs to a western species group united by the rectangular shape and serrate apex of the right paramere; slender, unforked ventral spicula and red-white dorsal color pattern. Males can be distinguished by the presence of a straight, elongate dorsal spine at the apex of the right paramere (Fig. 5).

Because of the common patterns of color variation between *nigridia* and sympatric species, females are difficult to identify. Females of *ute* Knight and *garryae* Knight lack erect, dark setae on the head and pronotum. In *taurina* Van Duzee the dark setae are much shorter and decumbent, and the embolium usually supports only pale setae. Females of *dakota* Knight have the second antennal segment strongly tapered distally. *L. chelifera* Knight is also solid red in eastern Colorado but has the anterior width of the pronotum narrower than *n. serica*, and western populations have white on the clavus. *L. marginata* Uhler can be distinguished only by its smaller size in areas of sympatry and white coloration on the clavus when present.

DISTRIBUTION.—*L. nigridia* is widely distributed throughout western North America, and the three subspecies display a largely parapatric distribution (Fig. 9). In the original description, Uhler (1895) listed this species from New Mexico and Arizona, states in which *nigridia* is not known to occur. Osborn (1898) reported *nigridia* from Iowa. This was clearly a misidentification, as at that time only the fuscous-white *n. nigridia* subspecies was recognized, and this form does not occur east of the Rocky Mountains.

REDESCRIPTION (Male).—Length 4.52–6.55; red to grayish fuscous; dorsum with erect, black setae and small, appressed sericeous setae. HEAD: width across eyes 1.01–1.29, vertex 0.61–0.76, vertically declivent, triangular; tylus produced, arcuate anteriorly, black; distance between antennal fossa and anterior margin of eye less than width of second antennal segment, antennal socket ringed in black; gena red; all sutures black; frons slightly convex, red, vittae black; vertex slightly concave, posterior margin black; basal carina usually distinct, lined with erect, black setae; posterior margin of head straight in dorsal view, postocular regions pale to rufous. ROSTRUM: length 1.53–1.78, black, dorsal surface slightly lighter; first segment rufous or

pale dorsally and laterally, reddish fuscous distally with black apex. ANTENNAE: black, fuscous, or red; I, length 0.40–0.64, with two large, stiff setae distally on the medial surface; II, 1.34–2.28; III, 0.81–1.50; IV, 0.35–0.51. PRONOTUM: length 0.65–1.29, posterior width 1.25–1.96, broadly convex, surface smooth, anterior angles rounded, lateral margins carinate, slightly arcuate in dorsal view, lined with erect, black setae, posterior margin straight or slightly sinuate; calli lightly infuscate to piceous, posterior angles broadly rounded, surrounded by fulvus or yellowish white; disc brick red to gray fuscous; propleura smooth, glabrous, episternum fulvus to white, sternum black. LEGS: black, testaceous, or fulvus; coxae and trochanters pale or fulvus; femora black on dorsum, paler on anterior and ventral surfaces, often spotted with fuscous, pale at apex; tibiae black or dark red, tarsi black. GENITALIA: *Tergal process*: relatively long compared with other species of *Lopidea*, evenly narrowed to a sharp point, slightly curved medially. *Right paramere*: roughly rhomboidal in outline, apex with long, erect spine; spine pointed or bifurcate at tip, straight or inclined toward base of paramere (Fig. 5). Apical edge of paramere slightly curved medially, usually with two vertical rows of small teeth; number and position of teeth variable. Small secondary spine occasionally present on dorsal edge near base of apical spine. Basal arm long, thick, curved medioventrally, apex variable, usually bifurcate (Fig. 6). *Left paramere*: sharply angled with apical lobe oval in lateral view. Medial flange distinct, separate from lateral flange for most of its length; narrow, elongate with distal end usually slightly expanded. VESICA: *Dorsal spicula*: short, lanceolate, straight or slightly curved, both margins of distal third serrate (Fig. 7). *Ventral spicula*: long, slender, slightly curved, a small swelling present near middle, apex with small teeth (Fig. 6). VESTITURE: head and pronotum with short, stiff, erect, black setae, black setae on hemelytra variable in length, suberect to erect, occasionally pale on light-colored area of corium, pronotum and hemelytra also with flattened sericeous setae, venter moderately covered with short, suberect pale setae.

FEMALE.—Similar in structure, color, and vestiture, but larger, broader, and more robust; frons more protuberant and broadly con-

vex than in male, vertex flat, basal carina less distinct, lateral margins of pronotum less carinate, hemelytra arcuate laterally. Length 4.82–7.46. HEAD: width across eyes 1.12–1.30, vertex 0.69–0.82. ROSTRUM: length 1.22–1.55. ANTENNAE: I, length 0.51–0.76; II, 1.48–2.49; III, 1.01–1.47; IV, 0.41–0.52. PRONOTUM: length 0.91–1.50, posterior width 1.42–2.17.

Lopidea nigridia nigridia Uhler

Lopidea nigridia Uhler, 1895:30 (n. sp., desc.).

Lopidea nigridea nigridea: Van Duzee, 1921:128. Henry and Wheeler, 1988:423 (cat.).

Lopidea rainieri Knight, 1965:8–9 (n. sp.). Henry and Wheeler, 1988:423 (cat.). *New synonymy*

Lopidea sculleni Knight, 1965:9 (n. sp.). Henry and Wheeler, 1988:424 (cat.). *New synonymy*

Lopidea rolfsi Knight, 1965:9 (n. sp.); Akingbohongbe, 1972:842 (note). Henry and Wheeler, 1988:424 (cat.). *New synonymy*

Lopidea wilcoxi Knight, 1965:11–12 (n. sp.). Henry and Wheeler, 1988:425 (cat.). *New synonymy*

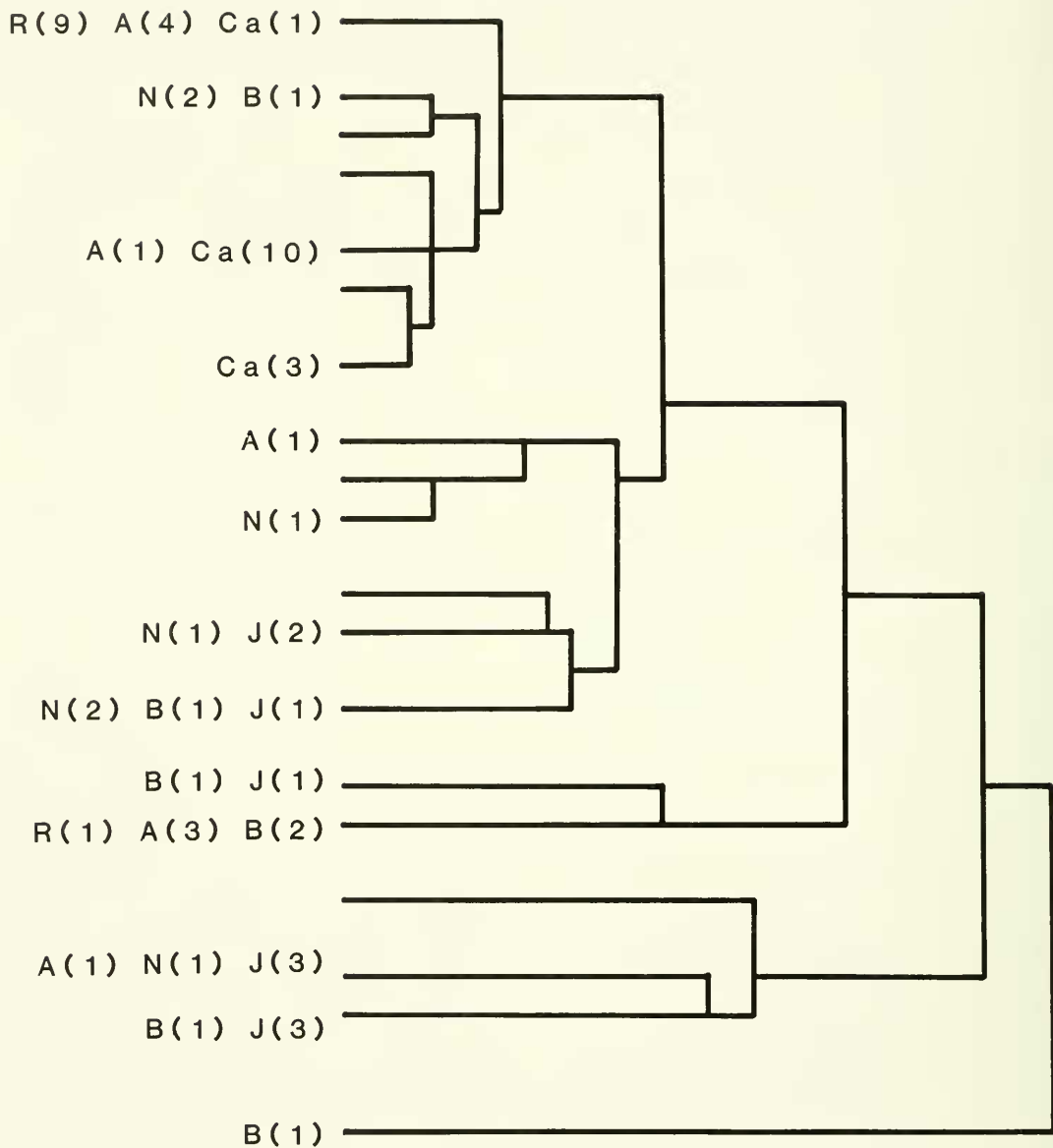
DIAGNOSIS.—*L. n. nigridia* Uhler is small to moderate in size, parallel sided, with a contrasting dorsal color pattern of smoky fuscous on the pronotum, scutellum, clavus, and most of the corium and pale white on the outer corium, embolium, and cuneus (Fig. 3A).

DISTRIBUTION.—*L. n. nigridia* occurs along the western slopes of the Rocky Mountains, throughout the Great Basin from southern Nevada and Utah to southern British Columbia. It is the common form along the eastern slopes of the Cascade Mountains and northern Sierra Nevada and occurs west of these ranges through xeric, low-elevation passes and river basins in California. *L. n. nigridia* also occurs throughout the coastal chaparral of southern California and into Baja California Norte. This subspecies inhabits the sagebrush-steppe habitat of the Great Basin, xeric mountain slopes, and dry lowlands. Its range appears to interdigitate with and superimpose on the ranges of the other two subspecies in some areas. However, the subspecies appear to be segregated by habitat in areas of sympatry, with *n. nigridia* inhabiting xeric shrub steppe or chaparral habitats and the other subspecies occurring in more mesic conditions, usually at higher elevations.

Lopidea nigridia aculeata Van Duzee,
new status

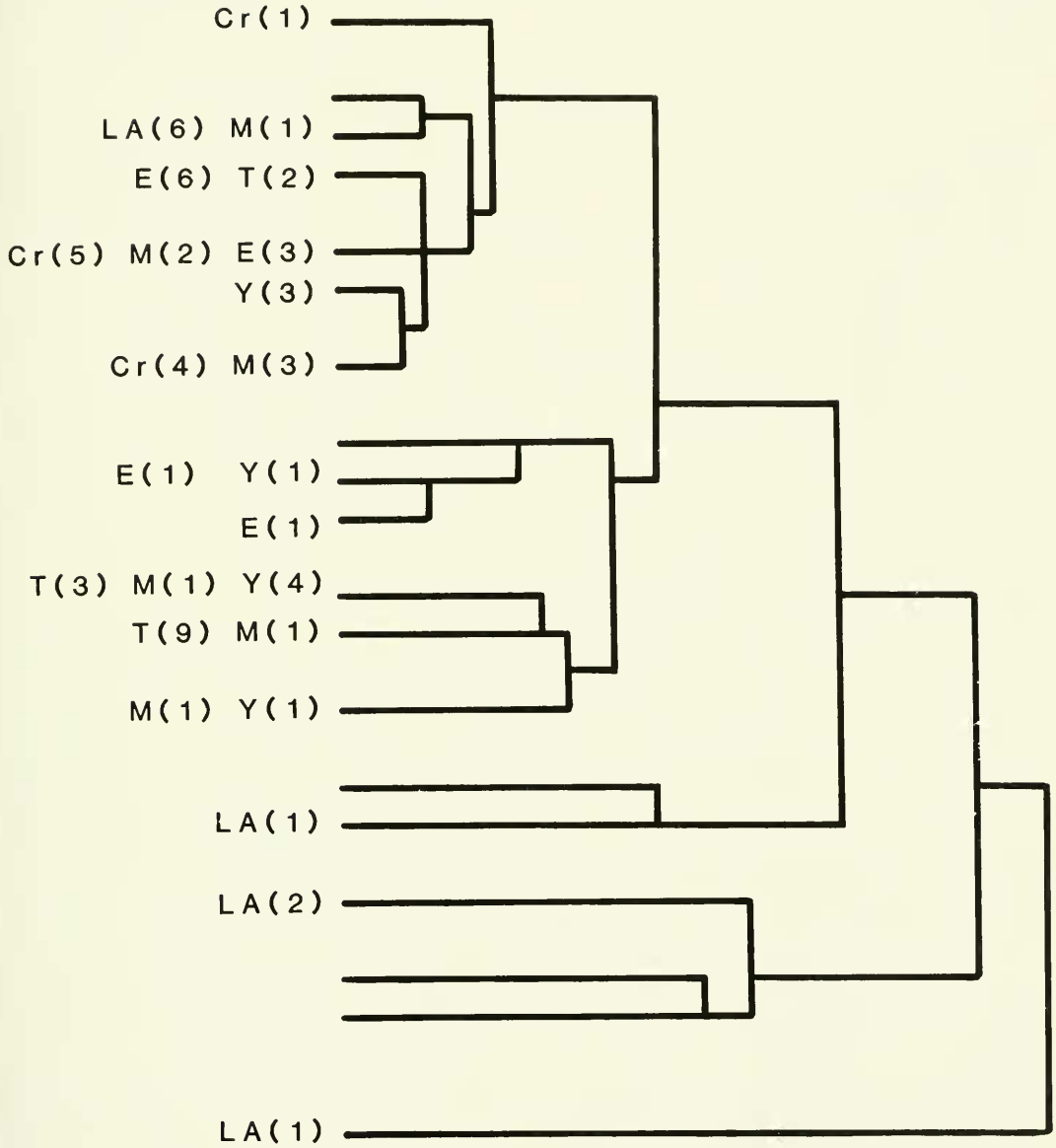
Lopidea aculeata Van Duzee, 1917:271 (n. sp.). Carvalho, 1958:83 (cat.). Knight, 1965:11 (color, dist.). Henry and Wheeler, 1988:417 (cat.).

A



Figs. SA–B. Results of UPGMA cluster analysis of color and paramere characters of 12 populations of *L. nigridia*. Letters represent populations; numbers represent the number of individuals from that population placed in that cluster. Both dendrograms are identical; to facilitate viewing and discussion, half the samples are shown on dendrogram A and the other half on dendrogram B. A, R = Mt. Rainier, WA (*L. n. nigridia*); A = Mt. Adams, WA (*L. n. nigridia*); Ca = Carbon Co., WY (*L. n. serica*); N = Elko Co., NV (*L. n. nigridia*); B = Baja California Norte (*L. n. aculeata*); J = Jackson Co., OR (*L. n. aculeata*); B, Cr = Crook Co., OR (*L. n. aculeata*); LA = Los Angeles Co., CA (*L. n. nigridia*); M = Mono Co., CA (*L. n. nigridia*); E = Elbert Co., CO (*L. n. serica*); T = Trinity Co., CA (*L. n. aculeata*); Y = Yosemite Park, CA (*L. n. aculeata*). A scale of distance values is not included because this analysis was not performed to measure morphological differences among OTUs but to illustrate groupings of OTUs using conventional taxonomic characters (see text).

B



Lopidea discreta Van Duzee, 1921:127 (n. sp.). Carvalho, 1958:84 (cat.). Henry and Wheeler, 1988:419 (cat.). *New synonymy*
Lopidea nigridea hirta Van Duzee, 1921:128 (n. subsp.). Carvalho, 1958:87 (cat.). Henry and Wheeler, 1988:423 (cat.). *New synonymy*
Lopidea fallax Knight, 1923:69 (n. sp.). Van Duzee, 1933:96 (note). Carvalho, 1958:84 (cat.). Henry and Wheeler, 1988:420 (cat.). *New synonymy*
Lopidea yakima Knight, 1923:69-70 (n. sp.). Carvalho, 1958:88 (cat.). Henry and Wheeler, 1988:425 (cat.). *New synonymy*
Lopidea usingeri Van Duzee, 1933:96 (n. sp.). Carvalho,

1958:88 (cat.). Henry and Wheeler, 1988:425 (cat.). *New synonymy*
Lopidea audeni Knight, 1965:9-10 (n. sp.) Henry and Wheeler, 1988:417 (cat.). *New synonymy*
Lopidea criogoni Knight, 1965:10 (n. sp.). Henry and Wheeler, 1988:420 (cat.). *New synonymy*
Lopidea calcaria Knight, 1965:11-12 (n. sp., note). Henry and Wheeler, 1988:418 (cat.). *New synonymy*
Lopidea chamberlini Knight, 1965:12-13 (n. sp., note). Henry and Wheeler, 1988:418 (cat.). *New synonymy*
Lopidea angustata Knight, 1965:12 (n. sp.). Henry and

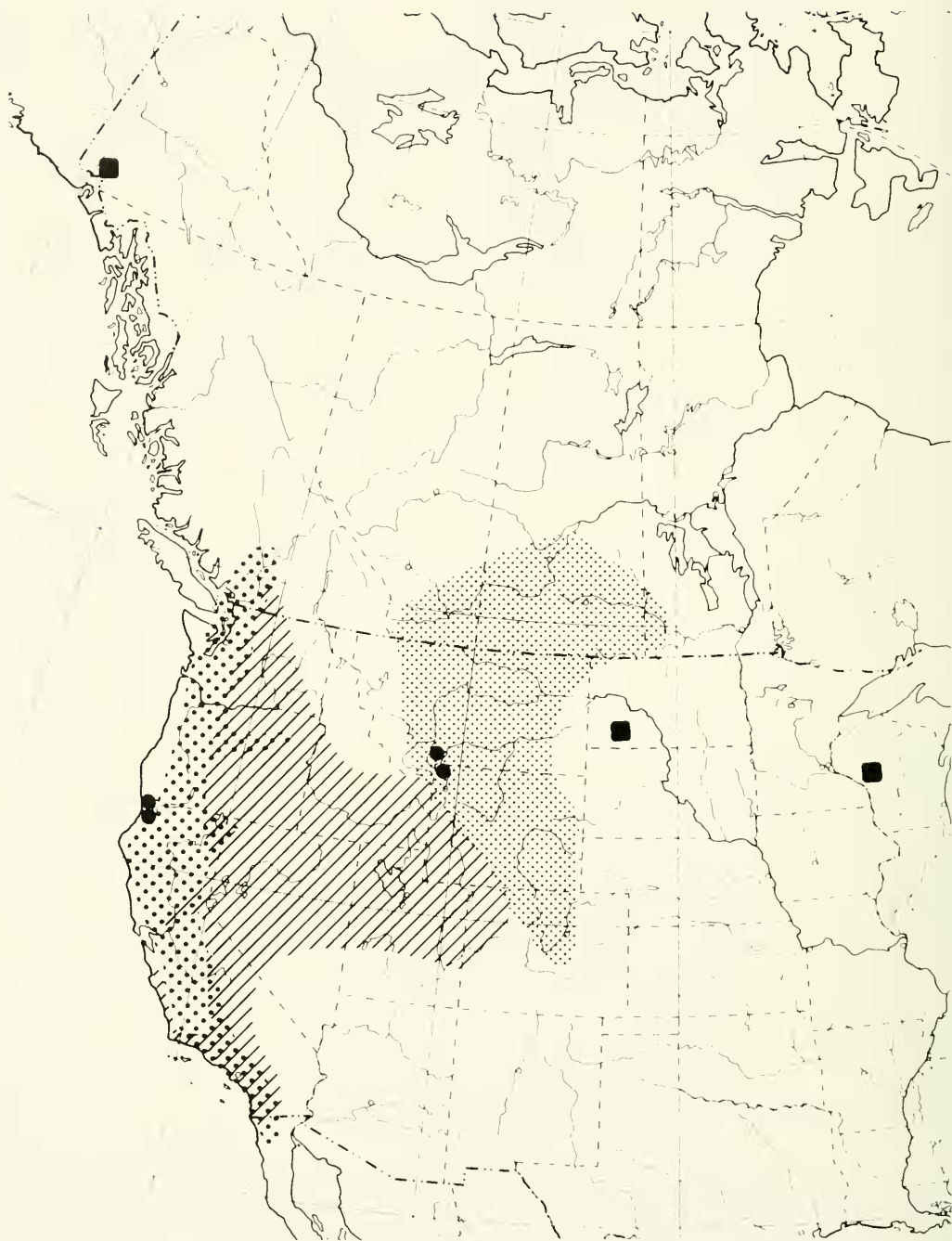


Fig. 9. Generalized distribution of *L. nigridia* Uhler. Small dots = *L. n. serica* Knight; large dots = *L. n. aculeata* Van Duzee; diagonal lines = *L. n. nigridia* Uhler; dark circles = additional localities for *L. n. nigridia*; dark squares = additional localities for *L. n. serica*.

Wheeler, 1958:417 (cat.). *New synonymy*
Lopidea rubrofusca Knight, 1965:13 (n. sp.). Henry and
 Wheeler, 1958:424 (cat.). *New synonymy*
Lopidea flavicostata Knight and Schaffner, 1968:75 (n.
 sp.). Henry and Wheeler, 1958:420 (cat.). *New*
synonymy

DIAGNOSIS.—*L. n. aculeata* Van Duzee is highly variable in size and coloration (Fig. 3B). It is usually larger than *n. nigridia* and often larger than *n. serica*, but it is always more linear than the latter. In the mountains of British Columbia, Washington, and Oregon it is solid red in dorsal coloration, with more yellowish individuals found at lower elevations. Northern California individuals show some white along the embolium and cuneus, this pattern increasing in distinctness and frequency in southern populations.

This subspecies is itself highly variable, and several distinct color forms can be distinguished as follows: (1) The type specimens of *aculeata* from Seattle, Washington, are yellowish with a dark head and a large hook at the posterior angle of the apex of the right paramere. The type material is representative of populations found at low elevations in the Willamette-Puget Lowland area of Washington and Oregon. (2) *L. n. hirta* Van Duzee was described from San Miguel Island off the coast of southern California. These specimens are solid red, small, and distinctly arcuate laterally. I have seen four males from San Miguel Island in the USNM. These specimens are larger and slightly less arcuate than the type specimens of *n. hirta*, but are still different from mainland populations at that latitude. (3) Specimens from the mainland of southern California are large and linear; most have a noticeably pale embolium and cuneus. Some populations from the southern Sierra Nevada, the San Gabriel and Santa Rosa mountains of southern California, are very distinct. The hemelytra are darker, almost fuscous, the disc of the pronotum is deep red and always shiny, and the setae, especially on the pronotum, are shorter and more decumbent. The type specimens of *discreta* Van Duzee are of this form.

DISTRIBUTION.—*L. n. aculeata* occurs in the Cascade Mountains of British Columbia, Washington, and Oregon, the eastern slopes of the coastal mountain ranges in these areas, and in the Blue and Wallawa mountains of Oregon and Washington. It occurs throughout the Coastal and Sierra Nevada ranges of

California. In southern California, however, the ranges of *n. aculeata* and *n. nigridia* overlap, and specimens intermediate and distinct in color pattern occur. Detailed studies of the local distributions of the color forms in this area are needed to clarify the problem.

Lopidea nigridia serica Knight, new status
Lopidea serica Knight, 1923:69 (n. sp.). Kelton, 1950:235
 (dist., hosts, fig., key). Akingbohunge, 1972:842
 (note). Henry and Wheeler, 1958:424 (cat.).
Lopidea medleri Akingbohunge, 1972:840–842 (n. sp.).
 Henry and Wheeler, 1958:422 (cat.). *New syn-*
onymy

DIAGNOSIS.—*L. n. serica* Knight is larger, more robust, with the lateral margins usually arcuate and solid red in dorsal coloration, except for black on the calli and light infuscation on the clavus (Fig. 3C). Females are usually submacropterous, with the membrane of the hemelytra reduced and barely reaching the end of the abdomen. Although this is the most morphologically distinct of the subspecies, it did not appear as such in the PCA because I did not use characters such as total length and maximum width of hemelytra.

DISTRIBUTION.—*L. n. serica* occurs along the eastern slopes of the Rocky Mountains from Alberta to Colorado and east across the northern Great Plains to southern Manitoba. It appears to inhabit the mesic grasslands of the eastern Rocky Mountains and short-grass prairie systems.

There are two interesting disjunct localities for *n. serica* in western Wisconsin and southwestern Yukon Territory and adjacent Alaska (Fig. 9). Although *n. serica* might be expected to occur in the relictual prairies of Wisconsin, the Wisconsin record comes from an area of scrub oak savannah. The Yukon records are from an area along the western edge of the Yukon Plateau and at the southern edge of the Alaska-Yukon glacial refugium. This record may represent a relictual population from the refugium or the tip of the post-Pleistocene northern migration along the Interior Plateau of British Columbia, although there are no other localities north of southern British Columbia. The host plants *Lupinus* and *Astragalus* are common to both the disjunct localities.

DISCUSSION OF SPECIES

Lopidea nigridia is the original spelling used in the description by Uhler (1895). This

clearly was not a *lapsus*, as I have seen Uhler determination labels using this spelling. The next citation to the species is Van Duzee (1914), who used the incorrect spelling of *nigridea*. All subsequent citations have also used the incorrect spelling.

There is confusion concerning the true identity of the species that Uhler referred to as *nigridia*. In his description (Uhler 1895), he described the color as brownish black with the outer border of the corium and cuneus rufulous or rufous, with no mention of white on the embolium or cuneus. However, this is clearly a contrasting dark-light pattern like that of the fuscous-white color form (*n. nigridia*). In addition, Uhler describes the anterior border of the pronotum as white, a pattern that occurs only in the fuscous-white form (*n. nigridia*) and not the red form (*n. serica*).

I located a fuscous-white specimen in the USNM bearing the label Colo. 1387. This number, 1387, corresponds with the following information in the C. F. Baker catalog: Steamboat Springs, Colo., July, C. F. Baker, ex. *Delphinium occidentale* (I attached a label with those data on the specimen). This information matches that given by Uhler for one of the specimens he examined for his original description. Knight (1923) illustrated the right paramere of another specimen from the type locality, and it is this concept of *nigridia* that has been used by all subsequent authors. Therefore, I have selected the former specimen as the lectotype of *Lopidea nigridia* Uhler and indicated such by attaching a label.

I have also seen specimens of *nigridia* with Uhler determination labels bearing the name *Lopidea obscura* Uhler, a Uhler manuscript name. It is possible that this is the name Uhler used for *L. n. nigridia*, and his description of *nigridia* referred to some other species with a contrasting light-dark color pattern. In addition, I have seen different specimens from the same locality identified by Uhler as both *nigridia* and *obscura*. It is likely, however, that the specimen I have selected as the lectotype was examined by Uhler in his description of *nigridia*.

DISCUSSION OF SUBSPECIES

Lopidea nigridia aculeata is highly variable and remains confusing to taxonomists. When

discussing *aculeata*, Knight (1965) noted that specimens collected from different areas in Oregon had identical parameres but varied from yellow fuscous to red fuscous and concluded that this species was variable in color. Van Duzee (1921), when describing *discreta*, commented, "It might be best to consider this a race or variety of *nigridea*." In his discussion of *usingeri* (Van Duzee 1933), he stated, "This species, like *obscura* exhibits considerable variation in the depth of coloration."

Knight distinguished *serica* from *nigridia* by the presence of golden sericeous pubescence in *serica*, but all specimens of *nigridia* (all North American *Lopidea*, in fact) have this pubescence if it is not rubbed off.

I have seen specimens that are topotypes of *rolfsi* Knight and *rainieri* Knight that Knight originally determined as *nigridia* Uhler and other fuscous and white specimens from Idaho determined as *nigridia* Uhler. Several specimens of intermediate color pattern from California have also been determined as *nigridia* by Van Duzee.

Lopidea rubrofusca Knight was described from a single male from Monticello, Utah, and is somewhat enigmatic. It is almost solid red, typical of *n. serica*. In size and development of the hemelytral membrane, however, it is more similar to *n. nigridia*; thus, I have synonymized it with *n. nigridia*.

Analysis of the ecology, behavior, habitat, and host preference in areas of sympatry may prove that the subspecies of *L. nigridia* are actually distinct species, but morphologically they do not display differences as great as those seen between other species of *Lopidea*. In addition, more detailed studies of the populations in some areas may suggest that some of the color forms within the subspecies deserve taxonomic recognition. With the available information, however, it is more prudent to recognize the structural similarity between these populations and the rest of *nigridia* and detail the geographic variation, rather than assign names to populations with distinct color patterns.

GENITALIA

I have weighted genitalic characters heavily in forming a species concept for *L. nigridia*. This is based on examinations of these structures throughout the genus and in related

Orthotylini. My analyses of paramere structure show no geographic pattern or distinction among subspecies. It is possible that incipient speciation has occurred in this complex and that it is not reflected in paramere morphology. This is most plausible for *L. n. nigridia* and *L. n. serica* in the northern and eastern parts of the range, where they retain distinct color patterns and exhibit the greatest differences in the shape of the dorsal spicula. Other species of Miridae also display geographic variation in size, vestiture, or color, including *Irbisia brachycera* (Uhler) (Schwartz 1984) and *Pilophorus tibialis* Van Duzee (Schuh and Schwartz 1988).

Although the parameres and vesicae have been used as taxonomic characters in the Miridae for at least 40 years, few studies have described the within-species variation of these structures. Stonedahl and Schwartz (1986) illustrate the variation in paramere structure for some species of *Pseudopsallus*. Stonedahl (1988) described clinal variation in the size and shape of the vesica of *Phytocoris yollabollae* Bliven and recognized two biotypes of *P. fraterculus* Van Duzee based on geographic differences in male genital structures. He found that other species of *Phytocoris* such as *P. tenuis* Van Duzee are highly variable in size, color, and genital structure; yet none of these variables were correlated with each other, nor did any show clear patterns of geographic variation. Detailed documentation of variation in genitalic structures is rare for any group of Heteroptera. Several examples are available for the auchenorrhynchous Homoptera, however. *Euseelis incisus* (Kirschbaum) exhibits seasonal variation (Muller 1954), and *E. incisus* Brulle shows temperature-induced variation (Muller 1957) of the aedeagus. Wagner (1955) illustrated extreme clinal geographic variation in the aedeagus of *Philaenus spumarius* (L.). Other studies have documented the intra- and inter-populational variation of aedeagal characters in this group (Wagner 1967, Le Quesne and Woodroffe 1976, Oman 1987). Studies of the infraspecific variation in spicula shape in the orthotyline Miridae are greatly needed. In *L. nigridia* the dorsal spicula varies from straight and blunt to curved and pointed (Fig. 7). The ventral spicula can also be twisted and varied in its curvature and dentation.

COLOR

The distinction between the subspecies in some areas and their discrete distributions probably reflects some degree of genetic segregation. This pattern might be interpreted as a species-level phenomenon; however, the subspecies are almost identical morphologically and do not appear to be segregated by host plant, as are other species of *Lopidea*. *L. n. aculeata*, however, shows inter- and intrapopulational variation in color pattern from fuscous-red or solid red to red-white.

Although I have placed subspecies determination labels on all specimens I examined for this study, the assignment of some populations to *L. n. nigridia* or *n. aculeata* is equivocal. For example, I have examined two series of specimens both collected from Mokelumne Hill, Calaveras Co., California, but from different years. One series exhibits the fuscous-white color pattern typical of *n. nigridia*, while the other series is a lighter red-white color typical of *n. aculeata*. There are a few additional localities from which two of the subspecies have been collected, although not from the same year or dates. Because of the lack of detailed local geographic variation, habitat preferences, and biological data from these areas, I refrain from making suggestions regarding hybrid suture zones and intergradation for these forms of *L. nigridia*. This suggests the possibility that these forms are not distinct lineages but only ecotypes.

Because temperature is known to affect the deposition of red and black pigments in Heteroptera (Knight 1924, Aldrich 1986), some of the color variation of *L. nigridia* is undoubtedly environmentally induced, and different color forms could develop at the same locality at different times of the year or different years. I have reared two of the subspecies, *n. nigridia* and *n. aculeata*, under three temperature regimes, 13 C, 21 C, and 33 C. Individuals of both subspecies reared at 13 C were clearly darker than those reared at 33 C; those reared at 13 C exhibited fuscous or black coloration on areas of the head, pronotum, and hemelytra that were red in the specimens reared at 33 C. However, the pale embolium and cuneus of the *n. nigridia* individuals were not affected by temperature, nor was the red color of these structures affected in the specimens of *n. aculeata*.

The pattern of color variation seen in *L. nigridia* is common in the genus *Lopidea*. Several other western species, such as *marginata* Uhler, *taurina* Van Duzee, and *chelififer* Knight, also have populations of solid red individuals and other populations with white margins of the hemelytra. The same distribution pattern of the *nigridia* subspecies is seen in other species with color polymorphism; the red-white or black-white forms occur in the Intermountain region, and the solid red forms occur further north and in the Rocky Mountains. It is also interesting that the distribution of the subspecies of *nigridia* corresponds to the distribution of other species of *Lopidea* of constant color. Species with contrasting red-white or fuscous-white patterns tend to predominate in the Intermountain region where the fuscous-white *n. nigridia* is found, and solid red or red-fuscous species are more common in the northern U.S. and Canada and the Great Plains where only the red *n. serica* occurs.

Other explanations such as host plant-induced color patterns (Palmer and Knight 1924a, 1924b) or selection for a certain pattern by different predator complexes (McIver and Lattin, in press) are equally viable.

BIOLOGY

The population biology of *Lopidea nigridia* Uhler in eastern Oregon was described in detail by McIver and Asquith (1989). At their study site, *nigridia* has one generation per year and overwinters in the egg stage in the tissue of its host plant, *Lupinus caudatus* Kell. Nymphs appear from late April to early June, most individuals achieving adulthood by mid-June. Oviposition is from late June through July, and most activity ends by early August.

In California, adults have been collected from 4 April to 1 September but are most commonly taken between 15 May and 15 July, with the average collection date being the third week in June. In other parts of the range adults emerge later in the season and are most common between 7 June and 15 August, with an average collection date in the second week of July.

Lopidea nigridia has been collected from at least 28 different genera of plants. West of the Rocky Mountains more than 48% of the host plant records are *Lupinus*. Testing this obser-

vation against a null hypothesis of an equal number of collections from all recorded hosts shows that *nigridia* is collected from *Lupinus* more often than would be expected by chance ($X^2 = 326.26$, $p < .001$, $N = 75$, $DF = 25$). In addition, four of five confirmed breeding records were on *Lupinus* and one on *Astragalus*.

In the Great Plains greater than 50% of the records are of *Astragalus*. This switch in host preference corresponds with the distribution of the subspecies *L. n. nigridia* and *n. serica*. Another mirid, *Coquillettia insignis* Uhler, which is typically associated with *Lupinus* in western North America, also feeds on *Astragalus* in Colorado and Wyoming (McIver and Stonedahl 1987). This pattern may reflect a change in the abundance and availability of the two host plants.

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